THE COLORS OF NORTHERN POLYPETALOUS FLOWERS.[1]

JOHN H. LOVELL.

ACCORDING to the later systems of classification the Apetalæ and Polypetalæ form a single subclass, the Choripetalæ. In the apetalous families of eastern North America, which have been considered in an earlier paper, there are 175 green, 89 white, 51 yellow, 45 red, and 24 purple flowers. The 1217 polypetalous plants have 140 green, 410 white, 333 yellow, 84 red, 193 purple, and 57 blue flowers. The northern Choripetalæ, then, contain 315 green, 499 white, 384 yellow, 129 red, 217 purple, and 57 blue flowers. Of the 92 families belonging to the Choripetalæ, 47 contain green, 52 white, 45 yellow, 28 red, 39 purple, and 5 blue flowers. The much greater abundance of species and families with green, white, and yellow coloration, as well as the less specialized structure of the flowers, points to these colors as more primitive or more easily developed than red, bright purple, or blue. In certain genera, however, small dull red and purplish flowers are evidently derived directly from the primitive green.

The order Ranales includes the Nymphæaceæ, Magnoliaceæ, Ranunculaceæ, and six other families of less importance. The simpler species of this order have the organs of the flowers spirally arranged, separate and distinct, and the stamens and pistils indefinite in number, as in Ranunculus. From the dominating character of the Ranales, says Engler, it is clear that the other orders of this series diverge from the Ranales in various ways, some following one direction of development, some another. The ancestral form of the angiospermous flower would appear to have been a branch, or part of a branch, with carpophylls at the end, followed by androphylls, and then by the primitive

[1] The Colors of Northern Monocotyledonous Flowers, *Amer. Nat.*, vol. xxxiii, p. 493; The Colors of Northern Apetalous Flowers, *Amer. Nat.*, vol. xxxv, p. 197.

leaves destined to form petals, sepals, and bracts. No such inflorescence now exists, but an approach to it may be found in the Magnoliaceæ. In Magnolia the floral bud terminates the secondary branches, of which it is only a prolongation. The oblong flower of the Magnolia has the receptacle prolonged and the parts of the perianth, the stamens, and the pistils, spirally arranged and indefinite in number. In the arrangement of the plant families in a lineal series, those flowers which have the organs separate and which resemble most closely the proangiospermous floral branch are regarded as the simplest; while the highest rank is assigned to those which have the organs modified and consolidated, as in the Orchidaceæ and Compositæ.

In the Nymphæaceæ, or water lilies, we meet with dicotyledonous plants resembling monocotyledons in the structure of the leaf and rootstock. The analogous arrangement of the fibrovascular bundles in a Nymphæa and a Tradescantia has been excellently figured by De Bary. The successive steps in which simple and distinct carpels may become compounded are also well shown by the genera of this family. In the primitive genus Nelumbium, also in the oldest forms found in a fossil condition, the simple carpels are contained in little pits in the large fleshy receptacle; in Cabomba and Brasenia the oblong carpels are borne on the receptacle, but are separate; in the fossil genus Anœctomeria of the Middle Tertiary the carpels are partially united; in Nymphæa the union is complete; and finally, the culmination is reached in *Victoria regia*, where the compound ovary is inferior. Of the eleven northern species four are white, five yellow, one red, and one purple. Yellow coloring was probably very early developed, as it is the color of the primitive *Nelumbo lutea* and of the three native species of Nymphæa (Nuphar). Throughout the summer the numerous broad shining leaves and large yellow flowers of *Nymphæa advena*, the large yellow pond lily, form a well-known characteristic in the vegetation of ponds and slowly moving streams. The six sepals are unequal: the three inner are large and bright yellow; the three outer and smaller are wholly or partially green exteriorly, though the upper half is often yellow, while the interior lower portion is reddish purple. The numerous petals are thick, short,

truncate, wedge-shaped bodies, which serve as honey glands. The honey is freely secreted on the outer side near the top, the nectariferous portion being orange yellow. The fruit is scarlet. I have collected upon the flowers in Maine four Diptera, two Coleoptera, and one small bee, *Halictus nelumbonis*, which confines its visits to this flower. Great numbers of the small fly *Hilara atra* revel in the pollen. The single species of Cabomba is white with a yellow base, and the northern species of Castalia (pond lily) are pure white tinged with pink, or deep pink in a variety growing in eastern Massachusetts. In the famous *Victoria regia* of the Amazon the outer petals are white and the inner crimson, and in *Nymphæa cærulea* of the Nile the flowers are blue. The leaves of several genera are strikingly bicolored, being light green above and violet or reddish purple below. According to Kerner the anthocyanin, or purple coloring matter on the lower side of the leaf, can arrest the rays of light (which would otherwise escape into the water) and change them into heat and make them useful to the plant.

The largest tree flowers known belong to Magnolia. "Their effect in early spring is grand beyond description, illuminating the whole landscape and filling the air with their rich perfume." The red flower of *M. campbellii* of Himalaya is ten to eleven inches broad, while *M. macrophylla* of the Southern States has flowers ten inches in diameter. Of the five species of the Magnolia four are white and one greenish yellow. *M. macrophylla* is white with a purple center, while *Liriodendron tulipifera*, tulip tree, is greenish yellow without and yellow within. *Magnolia grandiflora* is fertilized by rose beetles or Cetoniæ. At night the white flowers are 5° to 10° C. above the surrounding air, and thus afford warmth as well as food.

Both the Nymphæaceæ and Magnoliaceæ produce very large and conspicuous flowers, which are pollinated by the smaller bees, flies, and beetles. While these splendid showy flowers are, no doubt, of benefit for attracting the attention of insects, yet it is evident that they could be produced only by large trees and vigorous herbaceous plants. The water lilies grow in situations where the soil is charged with nitrogenous matter, and the framework of the plant requires a minimum of mechanical

support. The Magnolias are stately trees, growing in rich woodlands. Both families have very large leaves. The primitive color of the flowers was probably green, as it still is in *Magnolia acuminata*. Transition stages from green to yellow occur both in Liriodendron and in *Nymphæa advena*. In other instances, as in certain species of Magnolia and Castalia, they became white at a very early stage, and in certain species subsequently changed to red. In the case of *M. macrophylla*, where the white flower has a large purple center, the entire flower may have been purple, as in *Illicium floridanum*, or anise tree, or it may be a deposit of pigment resembling that found on the inner side of the sepals of *Nymphæa advena*.

In a part of the species of the Ranunculaceæ the petals are wanting; in a part they are small and transformed into hollow nectaries; while in others they are regular and conspicuous. The ancestral stock from which the various genera have diverged doubtless possessed petals, or phyllomes, corresponding to this whorl; but they had already been lost by some generic lines when insects began to visit the flowers. Of the ninety-seven species, six are green, twenty-six are white, thirty-eight are yellow, three are red, thirteen are purple, and eleven are blue. Conspicuousness is insured by the sepals in Clematis and Caltha; by the petals in Ranunculus; by both the petals and sepals in Aquilegia; and by the numerous stamens in Thalictrum, Actæa, and Cimicifuga. In Thalictrum the white or lilac filaments are broad and petaloid. The flowers are visited infrequently by flies and the short-tongued bees.

Of the apetalous flowers, *Caltha palustris* and *C. flabellifolia* have a yellow, and the aquatic *C. natans* a white, calyx. A change of locality may induce a change from yellow to white, as *Anemone alpina* on the Central Alps bears chiefly sulphur-yellow flowers, but in the eastern limestone Alps its flowers are always white. In our native species of Anemone the sepals are green, white, or purplish, but florists offer scarlet and blue varieties. The anthocyanin displayed by the underside of the sepals of *A. nemorosa*, especially in bud, probably serves to convert light rays into heat; this plant blooms in early springtime. The sepals of *Clematis ochroleuca* are green, of *C. virginiana*

white or greenish white; but in most species of Clematis the color is purple. By hybridization a great variety of hues have been produced, including blue, red, cream, and yellow. The calyx of Hepatica is white, rose, or blue. Kerner remarks that the flowers, which appear as soon as the snow leaves the ground in open woods, by their blue color present a strong contrast against the yellow-brown leafage, whereas in green meadows they would scarcely be seen. The occurrence of blue sepals is rare and is perhaps nowhere so well shown as in this family. From this brief survey of the coloring of the calyx it is evident that its capability for developing a wide range of colors equals that of the corolla. Though commonly green and only protective, it may give rise to any color.

In other genera of the Ranunculaceæ the petals are present but are transformed into nectaries. In Eranthis and Helleborus they take the form of a trumpet; in Isopyrum they are spoon-shaped, in Nigella lamp-shaped; in Coptis they resemble a hood, in Aquilegia a horn of plenty; and in Delphinium the two upper sepals and petals are both spurred. Tubular petals have also been observed in *Ranunculus repens* by Masters.[1] This tendency is inherent in the flowers and not induced by the agency of insects, and has greatly aided in the production of the different genera. The sepals of all these flowers are conspicuous. In *Helleborus viridis* the calyx is yellowish green, and in *H. niger*, or Christmas rose, which blooms in winter, the flowers are at first white, turning pinkish, and then green. *Trollius laxus*, which grows in the shade of dense swamps, has greenish-yellow flowers, while *T. europæus* has bright yellow sepals. *Coptis trifolia*, a woodland plant, has small white flowers in springtime.

The species formerly included in the genus Ranunculus, but now segregated into several genera, have the petals large and regular. The nectar is secreted in a little pit near the base. The thirty-one species of Ranunculus native in the northern states are yellow, or whitish in *R. nivalis*, or occasionally in *R. acris* in autumn. A wide range of colors is displayed by *R. asiaticus*, including yellow, red, purple, and nearly black.

[1] *Vegetable Teratology*, p. 23.

R. viridiflora is green, with scarlet edges. In *R. auricomus* the petals are sometimes wanting, and their place is taken by the sepals with their bright yellow limb. In *Ficaria ficaria* (*R. ficaria*) the petals are yellow, or red fading whitish. The white flowers of Batrachium, or water crowfoot, show that they are descended from ancestral yellow forms by retaining vestiges of this color as honey guides at the base of the petals. The cultivated *Adonis annua*, or pheasant's eye, has showy orange or red flowers, to which the black anthers offer a marked contrast. The most highly specialized regular flowers of this family belong to Aquilegia, or columbine. They may be regarded as the culmination of the buttercup type. The sepals are regular and petaloid, while the petals are prolonged backward into a hollow spur. The intermediate stages between the nectariferous pit of the buttercup and the hollow petal of Aquilegia are excellently shown in the extremely variable petals of *R. auricomus*. *Aquilegia canadensis* produces scarlet flowers, which are yellow inside and rarely all over, or occasionally they are white. There are two other species in the northern flora which exhibit a similar coloring, *Lonicera sempervirens* and *Spigelia marylandica*, and the former is sometimes yellow throughout. *A. canadensis* is visited by bumblebees and humming birds. The European *A. vulgaris* is blue, purple, or white.

The two zygomorphic genera, Delphinium and Aconitum, are the most recent in their origin, and represent the highest stage of development attained by the Ranunculaceæ. The sepals are petal-like. The flowers are blue or revert to white, or, in *Aconitum reclinatum*, are regularly white. High specialization, pollination by bees, and probably blue color, are here correlated. Masters gives an instance in *Delphinium peregrinum* of perfectly regular flowers having five sepals and five oblong stalked petals, and also in Aquilegia the tubular petals may be replaced by flat ones.

At the period when insects began to visit the flowers of the Ranunculaceæ, the different genera were in a transition state and only partially differentiated. It is evident that one effect of their visits was to render the flowers conspicuous. This result has been reached in different ways in the various genera, according

as the pigments have been deposited in the sepals, petals, or stamens. But while insects have been instrumental in developing bright coloration, the particular colors of the different species have been very largely determined by other conditions. The yellow of *Caltha palustris* and Ranunculus has probably been preceded by no other color than green. These flowers are visited by numerous flies, beetles, and the less specialized bees. Syrphidæ are abundant, a family of flies with many species, characterized by yellow markings, which would indicate that yellow was especially attractive to them. Müller states that he has seen *Eristalis intricarius* hover over the yellow flowers of Caltha, as the males hover over the females, then suddenly settle to suck honey or feed on the pollen. He also suggests that their love of yellow may have arisen from their visiting flowers of this color, and that sexual selection may have been guided by this taste. The white flowers of Batrachium have evidently passed through a yellow stage, but in other genera white or purple has been developed directly from the primitive green, as in Clematis. The blue flowers of Hepatica, Aquilegia, Delphinium, and Aconitum, which are very attractive to bees, appear to have passed through a yellow or white stage. The organs of the flowers of the Ranunculaceæ, according to Masters, more frequently revert to leaves than do those of any other family except the Rosaceæ.

The Berberidaceæ, Menispermaceæ, Calycanthaceæ, and Lauraceæ contain but few species. The shrubs of Berberis, or barberry, have the wood as well as the calyx and corolla yellow. The flowers are attractive to bees and flies. The foliage in autumn is yellow and crimson. The three white-flowered species of the Berberidaceæ occur in woodlands and bloom in May. The Menispermaceæ are woodland vines with small white flowers in panicles, or green in Calycocarpum, where the petals are wanting. The small flowers of the Lauraceæ are apetalous, but the calyx is yellow. The species are aromatic shrubs and trees.

The original color of the Papaveraceæ, or poppy family, was probably yellow. The sap also of many genera is yellow or red. The beautiful flowers of Papaver are yellow or scarlet, with a darker center. If the flowers contained nectar, this central

marking would be regarded as a honey guide, but as they are nectarless, and are visited by Andrenidæ and Diptera for pollen, it must have a different significance. It may be due to the more abundant nutrition received by the central portion. In the cultivated variety called Shirley the edges of the flower are white and the center is crimson. If a plant receive a check during growth by transplanting, the flower may revert to pure white. Such color contrasts, however, render the flowers more conspicuous. According to Kerner, honeybees do not visit scarlet flowers, either because they do not distinguish this color, or because it is unpleasant to them. In a garden in front of the house where he lived the scarlet geranium, *Pelargonium zonale*, and the narrow-leaved willow-herb, *Epilobium angustifolium*, were in bloom at the same time and not far apart. He observed that butterflies visited both indiscriminately; but the honeybee never paused in its flight over the scarlet flowers, though it frequently sought the red-purple flowers of the willow-herb. The flowers of Papaver are one to three inches broad, and hybrids are sometimes twelve inches in width. The flowers of Argemone, or prickly poppy, are also several inches in width. *A. mexicana* is yellow, rarely white, and *A. alba* is regularly white. *Sanguinea canadensis*, bloodroot, has a white flower and red sap; but the flower is sometimes pinkish, as is indicated by the name "red Indian paint." The genera Stylophorum, Glaucium, and Chelidonium have yellow sap and yellow flowers.

A group of irregular flowers formerly placed in a separate family, the Fumariaceæ, are now included in the poppy family. The species are fertilized by the long-tongued bees and flies. The heart-shaped pendulous flowers of Bicuculla (Dicentra), Dutchman's breeches, are white or pink. The smaller flowers of Capnoides (Corydalis) are pale yellow, while the larger are bright yellow. *C. sempervirens* is pink with yellow tips, and in bud is greenish white, while the European *C. solida* has the entire flower red. The influence exerted by insects upon the particular colors is very uncertain.

The Cruciferæ, like the Umbelliferæ, form a very natural family; the flowers closely resemble each other and differ chiefly, as Müller states, in the number and position of the honey glands

and in the situation of the anthers in relation to these and to the stigma. Many genera show evidences of retrogression in the small white flowers and in the regularity with which self-fertilization occurs. *Pringlea antiscorbutica*, which grows on the stormy shores of Kerguelen Land, where no winged insects can exist, since they would be swept into the sea, has reverted to wind-fertilization. In sheltered places the petals, which usually are wanting, are frequently present, and "on the same raceme some flowers may possess only a single petal, others two, three, or four; and the petals, though usually of a pale greenish color, are occasionally adorned with purple." This family is much less attractive to insects than the Umbelliferæ, and is visited chiefly by flies and the less specialized bees, such as Andrena and Halictus, and by a few beetles and Lepidoptera. Some flowers have no recorded visitors.

Of the 113 flowers, 2 are green, 54 white, 46 yellow, 1 red, and 10 purple; 20 of the 37 genera contain white and 16 yellow flowers, but only 4 genera contain both yellow and white. The white flowers are usually small, or even minute, and self-fertilized as in Subularia (awlwort), Lepidium (cress), and Bursa (shepherd's purse). The yellow flowers are larger, as in Sinapis and Brassica, and frequently show a tendency to change to white. In Rhaphanus (radish) the wild species, *R. raphanistrum*, is yellow, changing to white; while the garden radish, *R. sativus*, is white or pink. In Roripa (nasturtium) the two aquatic species are white, as well as the horse-radish, which grows wild along streams; the other species are yellow. In Draba four of the species are yellow and seven white, and *D. nemorosa* is yellow fading to whitish. In other species the calyx changes from green to yellow. It would seem probable that in these genera the white-flowered species have been derived from yellow progenitors; yellow appears to have been very early developed, and was not improbably the original color of this family.

The white flowers very frequently show a tendency to turn pink or purplish, and three genera contain both purple and white flowers. *Malcolmia maritima* has pink-red flowers, changing to violet purple. This transition is beautifully illustrated by the

rhizome of *Dentaria bulbifera*, which when taken from the earth is as white as ivory, but, if placed in a glass of water and exposed to the light of the sun, in a few days turns to a deep violet. The cultivated varieties of the genus Mathiola (stock, or gilly-flower), from Europe, present a wide range of colors, — as white, yellow, red, violet, and blue. The colors of Iberis (candytuft) are white, red, and purple; and the marginal flowers of this genus and of Alyssum and Dentaria have the outer petals enlarged, as occurs in the Umbelliferæ. *Hesperis tristis* has dark-colored flowers, visited at night by insects, which are attracted by the scent.

The inflorescence is in umbel-like racemes, which in fruit become greatly elongated. The central green buds and the surrounding flowers form a nearly flat surface and present a variety of color contrasts. Kerner has described several different classes. In *Draba verna* and *Thlaspi rotundatum* the green buds in the center are surrounded by two colored rings, — an inner one of small white flowers and an outer one of brown or purplish fruits, to which the petals, now enlarged to twice their original size, closely adhere. A variegated effect is thus produced. In *Thlaspi alliaceum* and *T. arvense* the flowers of the inner ring are white, but in the outer ring the green sepals have changed to yellow, while the fruit remains green. In a third group the inner ring is composed of flowers with colored petals, which in the outer ring have faded to white. In *Draba aizoides* there is a change from yellow to white, and in *Arabis cærulea* from blue to white. A fourth group is represented by *Æthionema grandiflorum*, in which the upper and under sides of the petals are differently colored. The flowers of the inner ring present the white upper side of the petals, but in the outer ring the petals have changed their position so that the red underside is now visible.

While the flowers of the Cruciferæ show that conspicuousness is correlated with the visits of insects, they furnish little evidence that particular colors have been evolved by the selective tastes of special insect groups. Both yellow and white flowers are visited by Syrphidæ, and they are also very frequent visitors to the inconspicuous but scented flowers of *Lepidium sativum*.

The blue flowers of *Arabis cærulea* are likewise sought by flies, while the nocturnal flowers of *Hesperis tristis* are dark-colored and dependent upon their fragrance. The parti-colored appearance of the flower clusters and the changes of color of individual flowers would indicate that the guests were a miscellaneous group of insects, with the color sense but feebly developed. How comparatively unimportant the color of a flower may become is well illustrated by *Lepidium sativum*. The small white flowers can be seen only a short distance, and in rainy weather do not expand. Yet they possess a strong scent, and Müller found them visited more frequently by insects than any other crucifer. Throughout the species of this family the petals have not been extensively modified either in form or color.

The flowers of the Capparidaceæ resemble those of the Cruciferæ both in form and color. *Polanisia graveolens* (clammy weed) has purplish sepals and stamens, and whitish petals.

There are three species of mignonette (Resedaceæ) in the northern states. The flowers are especially attractive to small bees of the genus Prosopis. These bees, which have an aromatic odor, are coal black, marked with yellow. They are doubtless attracted by the sweet fragrance, which can be perceived at a long distance. *Reseda luteola* (yellow weed) has greenish-yellow flowers and is cultivated for its yellow dye. *R. alba* has white flowers. In *R. odorata* the receptacle is at first yellow, changing to orange red; the petals are white or red, and the anthers red. The perfume is intense. On flowers growing in his window Müller collected five species of Prosopis, besides other insects. The strong scent of these flowers probably compensates for their small size and greenish colors.

The Sarraceniales contain two remarkable carnivorous families, the Sarraceniaceæ, or pitcher-plants, and the Droseraceæ, or sundews. The leaves, which are adapted to trap insects, are more conspicuous than the flowers. *Sarracenia purpurea* has purple-veined leaves and large purple flowers, while *S. flava* has green leaves and yellow flowers. The walls of the orifice, and the hoods, or lids, of the pitchers are the most highly colored parts. Leaves without ascidia or pitchers are green. The upper part of the pitcher of *S. laciniata* is pure white, marked

with a network of dark red veins. Of the five northern species of Drosera, four have white and one purple flowers. The red glandular leaves are far more prominent than the flowers. In the common *D. rotundifolia* the small white flowers open at midday, one or two at a time, and are visited sparingly by flies.

The order Rosales includes some thirteen families, differing but little from each other. The Saxifragaceæ, according to Engler, form the center of development, while the Rosaceæ and Papilionaceæ are regarded as sister families. The primitive character of many of the genera appears in the indefinite number of the stamens and pistils and their separate insertion upon the receptacle. The order, however, exhibits an advance upon the Ranales in that the carpels are more often united and the ovary inferior.

Of the Crassulaceæ, or orpine family, two species are green, two white, five yellow, two red, and two purple. The two green-flowered species have small flowers and grow in wet places, and in the case of *Penthorum sedoides* (ditch stonecrop) the petals usually are wanting. The genus Sedum (stonecrop) contains white, yellow, red, and purple flowers, with the honey readily accessible to short-lipped insects. In *S. acre* the leaves are yellowish green and the flowers yellow. While the blossoms are small they are produced in such profusion that they completely cover the plants, which grow in dense tufts and are sometimes called "golden moss." In *S. telephium* the petals are purple and often the entire plant. The honey is more deeply concealed than in the preceding species, and the flowers are in broad cymes, which are conspicuous and facilitate insect visits. In the species of Sempervivum the honey is still more deeply hidden and can be reached only by long-tongued insects. The cymose flowers are showy pink or purple. The petals of *Sempervivum wulfenii* are sulphur yellow with a purple base, and are pollinated by bumblebees. This purple coloring Müller believed to be a remnant inherited from a purple-flowered ancestor, from which the sulphur-yellow form, which is unlike the primitive yellow form of Sedum, had been developed by the selective influence of bumblebees. This color change is not improbable, for the petals of *Arnebia cornuta*, when they expand, are marked with dark

purple spots, which on the third day fade entirely away, leaving the flowers bright yellow. The colors of the flowers of the Crassulaceæ are often correlated with the colors of the stems and leaves.

The flowers of the Saxifragaceæ are small and arranged in racemes, cymes, and panicles, or solitary in Parnassia. The honey in most species is easily accessible, and the visitors are chiefly flies, which appear to have influenced the development of the coloring. To these insects white and yellow, marked or dotted with yellow, red, or purple, are thought to be especially attractive. The relation of Diptera to the flowers of Saxifraga is shown in the accompanying table compiled from Müller and Knuth.

Species.	Color.	Diptera.	Hymenoptera.	Coleoptera.	Lepidoptera.	Total.
S. rotundifolia .	White	14	1	—	—	15
S. stellaris . . .	White	12	2	1	1	16
S. aspera	White	2	—	—	—	2
S. bryoides . . .	White	9	2	2	—	13
S. aizoön	White	65	11	5	10	91
S. cæsia	White	15	3	3	3	24
S. exarata	White	4	1	—	—	5
S. muscoides . .	Greenish yellow	6	1	1	1	9
S. aizoides	Golden yellow .	85	20	8	13	126
S. oppositifolia .	Purple	4	—	1	3	8
Total		216	41	21	31	309

The genus Saxifraga is highly interesting because of the colored dots upon the corolla of many of the species. The white corolla of *S. rotundifolia* is sprinkled with round dots, the outer

of which are intense purple red; the inner are yellow, and the anthers white. The snow-white petals of *S. stellaris* are beset with purple dots and adorned with two orange-yellow spots. *S. aspera* and *S. bryoides* are white, with numerous shining yellow dots. *S. aizoides* has large golden-yellow flowers, marked with numerous orange-red dots; the nectaries and anthers are also yellow. This is the most conspicuous species of the genus and attracts 126 insects. *S. oppositifolia* has the honey more deeply concealed and is carmine or purple, and is diligently visited by butterflies. *S. hirculus*, of Labrador, is bright yellow with scarlet spots. In *S. michauxii* the three largest white petals have a pair of yellow spots at the base, but the two smaller are unspotted. The petals of *S. geum* are white, with a yellow spot at the base and several smaller purplish spots in the middle. As evidence that these markings are pleasing to Diptera, Müller states that he saw many specimens of two drone flies, *Sphegina clunipes* and *Pelecocera scævoides*, before sucking honey or eating pollen, poising before the dotted flowers of *S. rotundifolia* as if delighted by their appearance.

In his *Alpenblumen* Müller has tabulated his observations upon the relations of Diptera to the different colors of flowers. Most anthophilous species and families of flies made a much larger number of visits to white and yellow than to red and blue flowers. The Bombylidæ, which are suctorial only, showed a preference for red and blue to white and yellow in the proportion of 75 to 25; and the genera Volucella and Rhingia, of the Syrphidæ, showed a similar inclination in the proportion of $77\frac{2}{10}$ to $22\frac{8}{10}$. The less specialized Diptera were by far the most common on white and yellow; but as the proboscis increased in length and the species confined themselves more strictly to flowers, the percentage of visits to red and blue flowers increased from $14\frac{1}{10}$ in the Muscidæ to $29\frac{3}{10}$ in the Syrphidæ, and to 75 in the Bombylidæ. The Syrphidæ as flower visitors surpass all other Diptera, both in numbers and importance. The percentage of visits to yellow and white was $69\frac{7}{10}$, and to red and blue flowers was $29\frac{3}{10}$. The species marked yellow, whether short or long tongued, were two to three times as abundant on white and yellow as upon red and blue flowers. None of the Tabanidæ,

which do not restrict themselves to flowers, were observed on red and blue blossoms. Due consideration should be given to the limitation of the visits of flies by the form of the corolla, by scent, by the acuteness of the species in finding the honey, as well as by its adaptations and habits, and to the fact that in the case of several families the above conclusions are based on comparatively few observations.

Chrysoplenium alternifolium has no petals, but the sepals are bright yellow and the disk is also yellowish. Like the species of Saxifraga, it is visited chiefly by flies. The petals of Parnassia are white, with greenish veins. *P. palustris* is described as a "deceptive flower." It contains numerous yellow glandular bodies which appear like minute drops of honey, by which flies, especially Syrphidæ, are deceived. The flower contains a small amount of honey. In Hydrangea the cyme is made conspicuous by the enlargement of the calyx of the marginal flowers. In *H. hortensia*, cultivated from eastern Asia, the flowers are nearly all neutral and enlarged, and at first are green, changing directly to pink or purple. "The variable character of Hydrangea flowers," says a writer in the *Journal of Horticulture*, "when the plant is grown under certain conditions, has for many years been a sort of horticultural puzzle, which is still far from being satisfactorily solved. Plants with bright pink flowers, and those with flowers of a tolerably good blue, are not infrequently met with in positions near each other and apparently in soils exactly alike." A change of color in the flowers from pink to blue is sometimes caused by a change of soil, as the removal of a plant from a peaty soil to one of opposite character. The addition of iron to the soil frequently appears to produce the desired color change, though time is always required, the blue coloring not developing until the second year. *Saxifraga pennsylvanica* and *Heuchera americana* have green petals. Several species of Saxifraga are proterogynous, and the flowers in passing from the female to the male stage increase greatly in size.

The Grossulariaceæ (gooseberry family) contain only a single genus, Ribes. Of the northern species four are green, six white, one yellow, and two greenish purple. Most of the species are greenish in part. In *Ribes alpinum* the female flowers are green

and the male greenish yellow and much more conspicuous, though of no larger size. By this device insects are induced to visit the male, or pollen-bearing flowers, first. The petals of *R. sanguineum* change from white to pink, and of *R. aureum* from yellow to carmine. This color change, says Müller, also occurs in several species of Fuchsia and Lantana and enables the more intelligent bees to economize time by determining instantly those flowers which no longer contain nectar.

There are four green, thirty-five white, thirty-nine yellow, thirteen red, and four purple flowers in the Rosaceæ. The green flowers are small and apetalous, as in Alchemilla; the white flowers are very generally tinged or tipped with red, and vary from small in Spiræa to large in Rubus. Of the twenty genera in the northern states, twelve contain white flowers. Of the four species in Spiræa, three are white and one, *S. tomentosa* (hardhack), is rose, or rarely white. The flowers contain nectar and attract numerous flies, beetles, and Hymenoptera. Beetles are very frequent visitors to the small white flowers of *Aruncus aruncus*. The genus Rubus contains seventeen species, all of which are white except the purple *R. odoratus* and the pink *R. arcticus*. *R. strigosus*, or the wild red raspberry, has small, erect white petals, and the visitors are much fewer than to the blackberry, *R. villosus*. Though the flowers of the blackberry are also white, their increased conspicuousness secures them a much larger company of visitors, which is not far from one hundred. The petals are broad and flat, and the panicles large and numerous. *Dalibarda repens*, a woodland plant, produces both cleistogamic and open white flowers which are seldom fertile. The common field strawberry blooms in May and June, when the white blossoms contrast with the green meadow, and the growing grasses are as yet too short to conceal them.

Of the twenty-four species of Potentilla, two, *P. arguta* and *P. tridentata*, are white and are probably derived from yellow-flowered ancestors. They both grow in dry, rocky places. The other twenty-two species are yellow and are visited by small bees and flies. The prevalence of yellow coloring in this primitive genus would indicate its early development in the rose family. Yellow is also the color of *Duchesnea indica* (Indian

strawberry), which is certainly closely allied to the line of the field strawberry. *Waldsteinia fragarioides*, or the barren strawberry, which in leaf habit has the aspect of Fragaria, is likewise yellow. The simpler species of avens are yellow or white, while those with the honey concealed are purple. In *Geum rivale* (purple avens) the petals are purplish orange and the calyx brown purple. The honey can be reached only by long-tongued bees and flies, such as Bombus and Rhyngia. In *Comarum palustre* (marsh cinquefoil) the petals are purple and the sepals also inside. The plant grows in swamps and is visited by flies and less frequently by bees. The primitive color of both these species seems to have been yellow. The purple-flowering raspberry, *Rubus odoratus*, is however derived from white-flowered progenitors, for in New York at Pine Hill, Ulster County, a white-flowered form occurs, and the white species of this genus are frequently reddish or purple.

The ten species of Rosa in the northern states are rose or pink, varying to white. Though the flowers contain no honey, their color and fragrance attract many insects to the ample store of pollen. Several species have odors so peculiar that they may be recognized by them alone. The theory of Delpino that the distribution of this genus was determined by the range of certain families of Coleoptera has been disproved by the observations of Müller and others who have found bees very frequently upon the flowers. Beetles may often be collected, some species of which devour the petals bodily. The flowers of *Rosa canina* gain increased conspicuousness by always turning towards the sun. In Germany they are visited by eight beetles, six bees, and two flies.

The family of the Rosaceæ is very prolific in hybrids, and more than two hundred have been observed in nature. Innumerable hybrids of Rosa have been produced under cultivation which display countless combinations of yellow, red, and white, — as white tinged with yellow or pink, yellow fading to white or shaded with rose, or pink changing to white, rose shaded with yellow, or intense coloring such as crimson, carmine, and scarlet. In one variety on the same root there are produced every intermediate shade between white and red, and in another the colors

vary from yellow to crimson. There is no blue rose, but a white variety of *Rosa rugosa* from Japan has a bluish tinge. Blue does not, indeed, occur in this family. While red is common, none of the Rosaceæ are adapted to Lepidoptera. The visitors are a miscellaneous company of flies, beetles, and Hymenoptera.

This family exhibits a marked tendency in stem, leaf, bud, flower, and fruit to develop reddish coloration, — a tendency which is probably due to the chemical constitution of the sap. The smaller and less specialized Rosaceæ are yellow and white, and are visited by a variety of short-lipped insects. The increase of the white flowers in size and conspicuousness is usually attended by red coloration. Owing to the chemical constitution of the nutritive fluid, probably to its acidity (for when the petals of a rose are treated with ammonia they become blue), there has been no opportunity for the development of blue coloration by insects. With the enlargement of the perianth and the increased flow of sap, red tints have tended to appear by process of oxidation. The correlation of red coloring with an increased flow of the sap is well illustrated by the galls of the wild rose tree, which are often "as rosy as the rosiest apple." An abnormal flow of sap is caused to the part stung by the insect, and red coloration is due to the action of light, for it is of no service to the plant. Again, when the flowers of *Cratægus coccinea* are stung by the gallfly the different organs all become red, and the change in coloring is accompanied by an increase in size. In some instances, according to Darwin, red colors indicate greater vigor on the part of the plant, and I have also observed that the dwarfing of red flowers under cultivation may cause them to revert to white.

There is nothing more beautiful in the vegetation of the temperate zone than an orchard laden with expanding blossoms. The great quantities of flowers form billowing banks of whiteness, tinged with rose and flecked with the vivid green of the unfolding leaf buds, from which exhales the well-known sweet fragrance of the apple blossom. Of the Pomaceæ, or apple family, twenty-seven species are white and five red or partially white. The flowers are regular and usually clustered. Species

of Sorbus (mountain ash) and Cratægus (thorn) are very attractive to beetles, though often visited by flies and bees. The pear and apple are sought by fewer beetles and depend chiefly upon Hymenoptera and Diptera. The native species of apple are rose or pink, but readily change to white. The so-called bloomless apple has small green petals resembling sepals.

Twenty species of the Drupaceæ, or plum family, are white, and one, the peach, is pink. The blossoms of many plums appear in early spring in advance of the leaves and often completely wreathe the limbs. The flowers are visited by a great number of Andrenidæ, and in less than two hours I collected one hundred and twenty specimens on a Japan plum, and these were but a small part of those present.

The Mimosaceæ, Cæsalpiniaceæ, Krameriaceæ, and Papilionaceæ are often united in one family called the Leguminosæ, because the simple pistil becomes in fruit a legume. The Mimosa family connects the rose family with the Papilionaceæ. It is confined chiefly to the tropics, where the species are very numerous. The flowers are small, perfect, and regular, with the stamens distinct as in the rose family, or monodelphous as in the Papilionaceæ. In the northern species the colors are white, yellow, or pink. The filaments are long and threadlike, and are more conspicuous than the petals.

The pea, bean, clovers, vetch, and a whole host of leguminous allies are grouped together in the Papilionaceæ, — a name derived from the fancied resemblance of the flowers to a butterfly. Occasionally perfectly regular flowers occur by reversion, as has been observed in Laburnum. For the most part, nine of the ten stamens unite to form a tube, at the bottom of which lies the honey, if present; four of the petals interlock around this tube, while the fifth, called the "standard," is broad and erect and bright colored to attract the attention of insects. The flowers are fertilized by bees, which rest upon the wing petals, bracing the head against the standard and bringing the ventral side of the body in contact with the stigma and pollen. The irregularity of the flowers is due to their horizontal position and the unequal strains to which the petals are subjected. In the case of certain species bees alone are able to depress the keel

and obtain the nectar, and in their absence the flowers fail to set seed. Slight imperfections frequently permit flies and butterflies to steal the honey without rendering any service in return; and it has been suggested that the numerous species may be due to the efforts of the plants, metaphorically speaking, to remedy these defects.

The inflorescence is mainly in heads and racemes, but the effect of the individual flower cluster is often magnified manifold by the massing of the plants. In worn-out fields the vetch, *Vicia cracca*, often takes entire possession of the soil, forming large patches of purple blue. Similar effects are attained by the clover and wild lupine. Of the 197 species in the northern states, 39 are white, 33 are yellow, 13 red, 88 purple, and 24 blue. The predominance of blue and blue purple are believed to be due to the preference of bees for this color. The well-known experiments of Lubbock have shown that the honeybee can distinguish between colors. Scarlet, fire red, and all lurid colors are avoided by the honeybee. Blue, violet, and red are most attractive, followed by various shades of purple, yellowish white, and white.

An examination of the genera in which more than two species occur shows that they are rarely monochromatic; one or more species are usually differently colored from the rest. In Baptisia three species are white, two yellow, and one blue; in Trifolium (clover), four species are white, three yellow, four red, and three purple; in Psoralea two species are white, six purple, and three blue; in Astragalus seven species are white, three yellow, twelve purple, and one blue; and in Meibonia (tick trefoil), two species are white, one red, and nineteen purple. It is probably more advantageous in these genera for a part of the species to be of one color and a part of another than for all to be blue. When species are closely allied bees tend to visit them indiscriminately, as may be observed in the buttercups and goldenrods. But even in these cases they exhibit a preference to keep to a single species and would be greatly aided by differences in the coloring.

Many of the flowers of the Papilionaceæ in fading undergo a change of position and color. In the white clover the white

central flowers contrast with an older outer ring of rose-colored flowers. In the yellow clover the newer flowers contrast with a ring of chestnut brown. In *Vicia cracca* the older flowers bend downward and turn from violet blue to dark purple; while the purple flowers of Desmodium become green in withering. Striking color contrasts are also presented by the individual flower. The wings of the white corolla of *Vicia faba* (bean) are marked with two black eye-spots, and in the sweet pea and cultivated lupines the combinations of color are innumerable. *Astragalus vesicarius* has yellow blossoms in the Tyrol but violet on the limestone mountains of Hungary.

Nine families belong to the order Geraniales. In the genus Geranium of the Geraniaceæ the larger and more conspicuous purple flowers are visited abundantly by insects and have nearly or quite lost the power of self-fertilization. The smaller flowers are paler or white, attract few insects, and self-fertilization regularly takes place. *Geranium pratense* has been seen to produce on the same plant, when cultivated in a garden, both white and blue flowers. *G. robertianum*,[1] or red robin, has ribbed red-purple petals and, notwithstanding its disagreeable odor, is sought by bees as well as flies and beetles. In the pink flowers of *Erodium cicutarium* the upper petals are marked with dark lines, which serve as pathfinders. According to a series of forms figured by Knuth these markings vary greatly, from a few lines to spots and markings on all five petals.[2] In the genus Pelargonium from the Cape of Good Hope, this office of the upper petals becomes very highly developed; *P. tricolor* has the three lower petals white and the two upper crimson, each with a dark spot at base. The flowers of the Geranium always turn towards the sun.

Most of the northern species of Oxalis of the Oxalidaceæ are yellow and possess an acid juice, but *O. acetosella*, which grows in open woodlands, has large, pretty white flowers, veined with pink. It is sometimes called "wood sour," as druggists obtain from it salt of lemons. The plant is of social habit, and the flowers are quite conspicuous, yet are rarely visited by flies,

[1] Darwin. *Animals and Plants under Domestication*, vol. i, p. 404.
[2] Knuth. *Handbuch der Blutenbiologie*, Bd. i, p. 118.

beetles, or bees. Cultivated species of Oxalis are red or rose. *O. flava* is yellow, edged with red; and *O. versicolor* is white above and red beneath, so that the blossoms are white in the sunshine, and red when rolled up in the shade.

Like the Papilionaceæ, the flowers of the Polygalaceæ stand horizontal, and the petals are more or less united into a tube with a carina and alæ. The largest-flowered species is the fringed Polygala, *P. paucifolia*, which in spring produces beautiful rose-purple crested blossoms, with an occasional white variety. It is attractive to butterflies as well as bees. On the Alps, Müller found one species of Polygala fertilized entirely by butterflies. Most of our species have very small flowers, which are either greenish purple, or yellow changing to green in drying.

In the capability of the leaves to develop bright colors, and in the minute and reduced flowers attractive to Diptera, the Euphorbiaceæ, or spurge family, resemble the Araceæ, though it has not the remarkable adaptations for fertilization of Arum. The spurge family is of immense size and of very wide geographical distribution. The flowers are minute and have undergone much reduction. They are usually apetalous, and the entire perianth may be wanting, as in Euphorbia, where a single stamen represents a flower, and the flower cluster with its colored involucre was mistaken by the older botanists for a single flower. The genus Euphorbia is attractive to flies, though also visited by beetles and Hymenoptera; and in response to their visits the inflorescence in certain species possesses bright colors, honey, and a honey-like scent. The colors of many northern species are green, but a part are white, yellow, rose, or red. On *E. cyparissas*, the common cypress spurge, naturalized from Europe, and which has escaped from cultivation, the bracts are yellow. In the Alps, Müller collected twenty-one flies, one beetle, four Hymenoptera, and three Lepidoptera on the flowers, and in middle Germany he found many more Coleoptera and Hymenoptera. The genera Ricinus and Croton are extensively cultivated for the tropical aspect of the magnificent foliage. *Ricinus communis* is anemophilous.

In the order Geraniales, to which the families just considered belong, and in the succeeding order, the Sapindales, the flowers

mark an advance upon the Rosales in that the cyclic arrangement prevails and there is an imperfect union of the carpels. The families of the Sapindales differ widely and have been divided into numerous subseries. The Empetraceæ, Buxaceæ, and Limnanthaceæ are represented in the northern states by only four species. The flowers are small, and probably partly primitive and partly reduced.

The Anacardiaceæ and a number of allied families are of much interest, as the inflorescence has been but little modified by insects. The species are mainly trees and shrubs with green, white, and greenish-yellow flowers, which are visited by Diptera and the smaller and less-specialized Hymenoptera. The Anacardiaceæ, or sumac family, have small, regular flowers in dense panicles. Both the sepals and petals are present, but the flowers are greenish or greenish yellow, though sometimes tinged with red as in the smoke tree. They secrete honey and are attractive to flies and Andrenidæ. On the smoke tree, *Cotinus cotinus* (*Rhus cotinus*), there have been collected six flies, one beetle, and ten Hymenoptera. The species tend to become diœcious, and *Cotinus cotinus* (*Rhus cotinus*) shows all transitional stages between staminate, hermaphrodite, and pistillate flowers. While the visits of insects have not developed bright colors, the leaves of *Rhus radicans* and the fruit of *R. aromatica* are red in autumn, and the wood of several species is orange yellow. *R. glabra* sometimes has the whole or a part of the flower cluster changed into small leaves.

The various species of Illicaceæ, or holly, have small white flowers, with freely exposed honey. The berries of *Ilex verticillata* are bright red, or rarely yellow, or even white. The visitors are similar to those of the preceding family. The Celastraceæ is composed of trees and shrubs with small, regular, green, yellow, and purple flowers.

Five species are green, three yellow, and one red in the Aceraceæ, or maple family. The green flowers of *Acer saccharinum* are without petals. In *A. rubrum* (red maple) the diœcious flowers are crimson, and the visitors are Andrenidæ and Diptera. There is no reason to suppose that the crimson coloring has been developed by insects, for the entire flower, the leaf

buds, the young leaves, and the twigs are of this color, while the bark yields a purple dye. The flowers appear in early spring before the leaves and were formerly anemophilous. *A. spicatum* blooms later, and the compound racemes of greenish-yellow flowers are large and erect. Müller states that dull-yellow flowers are avoided by beetles, but I have observed many beetles, as well as bees, upon the inflorescence of this species. Closely allied to the maple, but of more recent origin, is the genus Æsculus. The flowers seem to have possessed special capabilities that led to their adaptation to bumblebees. Among ornamental trees few present a more stately and splendid appearance when in blossom than the common horse-chestnut, *Æsculus hippocastanum*. It has large white flowers in crowded panicles, with the petals marked with yellow, which in a few days changes to orange and then to crimson. I have observed the honeybee, four species of Bombus, and one Andrena as visitors. Of the four other species of this genus three have yellow petals, and one, *Æsculus pavia*, bright-red flowers an inch in length.

Impatiens biflora, of the Balsaminaceæ, is orange yellow, spotted with reddish brown. One of the petals forms a spurred sac. August 10 I examined a large number of flowers; none of the spurs were perforated, and they were visited legitimately by *Bombus vagans*, which made from seven to twelve visits per minute. August 23 and 27 I found hundreds of the flowers perforated, and both honeybees and bumblebees stealing the nectar. If the Impatiens, fitly called "touch-me-not," could speak, what a protest it would utter! Various Diptera are attracted to the outside of the sac by the bright colors.

The colors of the Vitaceæ, or vine family, are green, closely resembling the foliage, and depend entirely upon their strong fragrance to attract insects. The inflorescence is in dense panicles. The calyx is minute, with the limb nearly obsolete. The green valvate petals form a hood over the stamens and never expand, but fall away by separating at the base and coiling spirally upward. The odor, which resembles that of mignonette, can be perceived at a long distance. "In a journey up the Danube," says Kerner, "through the part of the valley called the Wachan, with its vine-clad slopes, I found the air of the

whole valley, even that above the water, so filled with the scent of vine flowers that it seemed almost impossible they should be so far off. And yet the nearest vines on the banks were one hundred yards above the water and at least three hundred yards from the boat. Afterwards I found, when wandering through the vineyards, that the smell of the flowers close at hand was much weaker than at a distance, and was forced to the paradoxical opinion that with increasing distance and diffusion over a wider area the scent does not diminish but waxes stronger." Under cultivation the species are usually perfect, but when growing wild are mostly unisexual. Cross-fertilization, according to Knuth, is occasionally effected by the wind. As visitors to the flowers of *Vitis vinifera* there have been observed the honeybee, and various species of Halictus; while of Coleoptera, notwithstanding the green flowers, there have been enumerated twenty-one species. Müller's statement that "beetles are only or mainly attracted to flowers by bright colors" does not agree with the many species observed on the flowers of the vine.

Union of the carpels prevails in the order Malvales, which includes the two families Tiliaceæ and Malvaceæ. A part of the genera with the carpels distinct, or but slightly united, still preserves a more primitive stage in the evolution of the flower. As in the vine family, the flowers of the linden, or lime tree, depend on their strong scent, rather than upon their coloration, to attract pollinators. The greenish-white flowers of *Tilia americana* are in small, drooping, cymose clusters, sheltered beneath a floral bract. The thickened concave sepals secrete and contain the honey, which a pubescent fringe prevents from escaping. A high value is placed upon honey made from the linden; in some localities the leaves are also covered with a copious secretion of a sweet liquid, and sugar has been made from the sap. The strong scent, which is more noticeable at a short distance than close to the tree, is very attractive to the honeybee, many of which I have seen at work on the flowers in Maine. On *T. ulmifolia* in Germany Müller and Knuth collected eleven flies and seven bees. The absence of beetles I attribute not to the dull color of the petals, but to the inaccessibility of the drooping inflorescence, covered both by the leaves and the floral

bract. The leaves of a part of the species are bicolored, green above, and white, because densely woolly, beneath.

One-half, or thirteen, of the northern species of Malvaceæ are pink or red, four are red purple, five yellow, and four white. No other polypetalous family has so large a percentage of the flowers red. Both in temperate and tropical regions the blossoms are remarkably large and showy, and are usually yellow or red. The chief agents in intercrossing are bees. *Malva rotundifolia* has white flowers striped with pink, and slender pink stigmas, while *M. moschata* has either pink or white blossoms. The marsh mallow, *Althæa officinalis*, well known for the use of the mucilaginous root in confectionery, has pink flowers an inch broad; and *A. rosea*, the hollyhock of the garden, displays white, yellow, rose, crimson, purple, and black hues. A single species of Abutilon with yellow flowers has become naturalized from Asia. In South America the natural fertilizers of Abutilon are humming birds. The genus Hibiscus consists of splendid flowers of immense size. In color they are yellow, red, or white; the yellow forms have a purple or blackish eye, and the red a dark center. The common cotton, *Gossipium herbaceum*, one of the most valuable of nature's plant productions, has yellow petals, and the floral and extra-floral nectaries attract many insects as well as the ruby-throated humming bird.

Within the order Parietales the placentæ are parietal; "and the floral evolution," says Engler, "has already reached very complicated floral types." The Theaceæ (tea family) is mainly of tropical distribution, consisting of shrubs or trees with large solitary white flowers. Three species occur in the southern states. The handsome white flowers of *Stuartia malachodendron* have purple filaments; in *S. pentagyna* the petals are cream color and the sepals reddish outside. To this family belong the tea plant and the Camellia.

The Hypericaceæ have nearly monochromatic flowers, as twenty-two species are yellow and two red. The larger flowers of Hypericum are bright or orange yellow, as *H. ascyrum*, while the smaller are often pale yellow. The leaves, sepals, and petals of *H. maculatum* are sprinkled with numerous black dots. *H. perforatum*, introduced from Europe, contains no honey, but

the large, black-dotted, bright-yellow flowers attract many flies, which feed on the pollen. The smaller-flowered species are rarely sought by insects, and self-fertilization is possible throughout the genus. The two small, reddish-flowered species belong to the genus Triadenum. The petals of *Triadenum virginicum* are rose colored, with deeper veins, and do not exceed the calyx; the honey glands are orange and the anthers bright yellow with white filaments. The flowers are very sparingly visited by insects, and after repeatedly watching them I have observed only two bees and three flies. The stem, the capsule, and often the leaves are a deep crimson, as is often the case in Hypericum. The change in the petals from yellow to red is probably correlated with the red coloration of the plant rather than due to insect selection. In *Hypericum perforatum*, which frequently has the foliage crimson colored, the yellow petals are tinged with rose in the bud, which fades away as the flower opens. In *Epilobium palustre* reddish flowers are more common when the stems are red than when they are green.

In the Cistaceæ, or rock-rose family, the genus Helianthemum (frostweed) has large yellow flowers, which throughout the day follow the sun. They are ephemeral, but the plants remain in blossom for a long time, as there is a succession of flowers, as in the crucifers. There is no honey, but the pollen attracts a miscellaneous company of insects. As is frequently the case in pollen flowers, pollen falling from the anthers is not lost but lodges in the concave petals. The small greenish flowers of Lechea (pinweed) are self-fertilized.

The violet family in the northern states contains 7 white, 6 yellow, 4 purple, and 17 blue flowers. About 300 species of this family and 150 of the genus Viola have been described. Müller regards yellow as the original color of the violets. The small, short-spurred *V. biflora*, which in the Alps is fertilized by flies, has yellow flowers; the large-flowered *V. tricolor*, variety *alpestris*, presents all stages in the passage from yellow to blue. "Many plants have flowers which are yellow throughout; in others the flowers are yellow when they open but change gradually to blue; and in others the change to blue occurs immediately after opening, or even before." *V. calcarata*, which has a spur

from 13 to 25 mm. in length and is fertilized by Lepidoptera, chiefly by *Macroglossa stellatarum*, displays, according to Kerner, in the meadows of the western Alps a blue corolla, and a yellow corolla in the eastern Alps. Darwin transplanted a large, uniformly colored, dark-purple variety of the pansy while in full flower, and it subsequently produced smaller flowers, with the lower petals yellow. The white forms appear to be derived from blue progenitors, for the former are purple veined and may be tinged with violet. Blue species of Viola which often have white flowers are *V. palmata*, *V. obliqua*, and *V. odorata*, and in various stages *V. canadensis*. Pathfinders among white northern polypetalous flowers are of infrequent occurrence. The most prominent instances are *Saxifraga michauxii*, with three of the unequal white petals marked with yellow; *Oxalis acetosella*, white with reddish veins; Parnassia, with greenish veins; *Magnolia macrophylla*, *Æsculus hippocastanum*, *Lespedeza hirta*, and *L. capitata* display purple spots. In the white violets the purple honey guides are highly developed, which may be best explained by supposing them descended from blue-flowered ancestors with darker veins similar to existing species.

The beautiful and richly variegated varieties of *V. tricolor*, the garden pansy, are due partly to selection and partly to hybridization. The corolla may be pure white, yellow, red, blue, purple, or black; or there may be combinations of yellow and blue; yellow and red; yellow, blue, and white; and blue and white. According to Strasburger, in the pansy the cells of the epidermis of the petals contain both violet sap and yellow granules. "The striking diversities in color presented by different parts of a given petal depend wholly upon combinations of these two elements of color, — namely, violet sap and yellow granules."[1] Places which are devoid of both these elements are white, as the light is refracted and reflected by the intercellular spaces containing air. When sections of white roots of a violet plant are exposed to the air they change to violet; and the leaves of *V. cucullata* when grown at alpine altitudes become yellow.

While the violets vie with the roses in popular favor, they do not prove attractive in an equal degree to insects. In Maine I

[1] Goodale. *Physiological Botany*, p. 170.

have rarely observed visitors to the white and blue varieties, but on the yellow *V. rotundifolia*, which blooms early in May, I have seen many bees belonging to the genera Bombus, Nomada, and Andrena. Besides the conspicuous flowers, which are often unfruitful, many species produce cleistogamic flowers, in which the petals are reduced to mere scales, but the green sepals remain essentially unchanged. Occasionally the violets bloom a second time in late fall.

The failure of the yellow plastids to develop and the predominance of the colored cell sap produce blue flowers, and the non-development of both color elements results in white blossoms. In these color changes other ecological factors are more important than insects. For instance, of the yellow-flowered species one is visited by flies, another by bees, and the either yellow or blue *V. calcarata* is adapted to Lepidoptera.

The passion flowers are mostly natives of South America and are fertilized by humming birds and bumblebees. The calyx of the common *Passiflora cærulea* remains green until it has attained nearly its full size, when it changes to blue and white; the petals are white; the outer corona consists of several rows of blue filaments banded with white, but the inner corona is smaller and unmarked. Fritz Müller considered the coronæ to be of service in detaining small insects and keeping them caged for humming birds.

The Cacti, of which over a thousand species are natives of America, are especially abundant on the sandy plains of Mexico. The nearest living representative of the ancestral stock of this family is the genus Pereskia, which still possesses leaves of the usual form. "The earliest derived line was Opuntia. From the primitive Opuntia forms the columnar Cereus line was derived, with its numerous generic branches and diverse habits. Low down upon the columnar Cereus line the Echinocactus line branched out, which gave rise later to Mamillaria and still later to Anhalonia" (*Botanical Gazette*, Vol. XXVII, No. 3, p. 228). The flowers of the Cacti are solitary and sessile, with the sepals and petals and stamens numerous and spirally arranged. In size they are usually large and showy, as in *Cereus grandiflora*, queen of the night, where they are 20 cm. in diameter. In Pereskia

the flowers are white or yellowish; in Opuntia yellow, or in *O. opuntia* and *O. humifusa* yellow with a reddish center; in Cereus in the nocturnal forms white, in the diurnal species red or crimson; in Echinocactus yellow, white, and crimson; in Mamillaria yellow, pink, white, and purple; and in Anhalonia white, rose, and purple. The spines of the Cacti are often very beautiful objects and exhibit a great variety of color, as white, black, yellow, red, and purple. The stems, while usually green, are frequently nearly blue; the fruits are green, red, and purple.

The Thymeleaceæ and Eleagnaceæ in the northern states have no petals, but the calyx is enlarged, prolonged into a tube, and colored yellow, red purple, or white. In Europe *Daphne mezereum* has the red-purple flowers visited by long-tongued bees, flies, and butterflies; in the Alps the white or red flowers of *D. striata* are strong scented in the evening and are visited by moths.

The petals are wanting in the single green species of the Lythraceæ, or loosestrife family, *Didiplis diandra*, which has minute solitary flowers. The loss of the corolla is doubtless due to retrogression. In Ammannia the flowers are small and the purple petals fall away as soon as they expand, and in the southern *A. latifolia* they are wanting. The purple flowers of Lythrum vary from small to large. The eighteen possible ways of fertilization in the red-purple trimorphous flowers of *Lythrum salicaria* were made the subject of a long series of laborious experiments by Darwin, which resulted in breaking down the last barrier between species and varieties. It is a singular fact that the pollen of the longest stamens in this species is green, and of the middle-sized and shortest, yellow. The legitimate fertilizers are long-tongued insects. In Parsonia, or Cuphea as it is better known, the flowers are pink or crimson, and in a cultivated species from Mexico, *C. platycentra*, there are no petals, but the tubular calyx is bright vermilion with a violet border.

The Melastomaceæ are represented in North America only by the genus Rhexia, with handsome purple or yellow flowers. The family is most abundant in South America. In Heeria a part of the stamens are devoted to rendering the flowers conspicuous and a part to producing pollen. *Cyanophyllum*

metallicum, from Central America, has magnificent leaves, purple beneath and metallic blue above.

In the Onagraceæ, or evening primrose family, there are three green, fourteen white, twenty-four yellow, ten red, and six purple flowers. The three small green flowers belong to Ludwigia, and the petals are either minute or absent. Many of the white flowers show a tendency to change to pink or red. The large white flowers of the three northern species of Anogra all turn pink with age. Several species of Gaura also change to red. *G. coccinea* is red, turning scarlet in fading. The two species of Circæa (enchanter's nightshade) are delicate, colorless little plants, which grow in damp, shady woods and have small white flowers, fertilized by flies. The yellow flowers are in part diurnal and in part nocturnal as in *Onagra biennis*. Yellow is a much rarer color than white in flowers expanding at night.

With a single exception the flowers of Epilobium are red or red purple. *E. angustifolium*, called "fireweed" (as the plants spring up in abundance in newly cleared or burnt lands), has very conspicuous flowers in long, terminal racemes. The sepals and petals are purple red, except the lower sepal, which is white, and rarely the whole flower reverts to white. The pollen is greenish purple, and the stems and seed vessels are purple. Honey is secreted by a green, fleshy ring at the base of the style. Bumblebees are the most important agents in intercrossing and will visit as many as thirty-seven flowers in a minute. I have collected on this species twenty-one Hymenoptera, five Diptera, three Lepidoptera, and two beetles. In the smaller species of Epilobium, such as *E. palustre* and *E. lineare*, the small flowers are reddish or white, both kinds occurring on the same plant. When the stems are purple the flowers are more often red than when the stems are green. There are few visitors, and self-fertilization regularly occurs. The only northern white species of Epilobium is *E. alpinum*, which has small white flowers which are regularly self-fertilized. In *E. hirsutum* the four white stigma lobes form a cross on the red field of the petals.

The exotic genera deserve special mention. In *Lopezia racemosa*, from Mexico, there are on two of the petals dry,

shining, yellow bodies, which appear like drops of honey and are deceptive to flies, like the mock nectaries of Parnassia. The species of Fuchsia are confined chiefly to the shady forests of Central and South America. Both whorls of the perianth are highly colored, the calyx and stamens crimson or scarlet, and the petals purple or red. The flowers are pendulous and visited by humming birds. Crimson or scarlet flowers are not common where there are no humming birds. Kerner calls attention to the rarity of scarlet in south Europe compared with its frequent occurrence in tropical America, where in the primeval forests there are a great number of scarlet or fire-red species of Begonias, Fuchsias, Lobelias, Erythrinas, Salvias, and other crimson blossoms, which are surrounded by humming birds. Many hybrids of Fuchsia have arisen under cultivation. The earliest white-sepaled form was produced in England in 1822, while the first white corolla was secured in 1853.

In the Haloragidaceæ, or water-milfoil family, the petals are small or wanting and the flowers are wind-fertilized. The species are mainly aquatic.

The last of the polypetalous orders is the Umbellales, which includes the Araliaceæ, Umbelliferæ, and Cornaceæ. The flowers are small and densely aggregated in umbels, cymes, and panicles. In the ginseng family, or Araliaceæ, the flowers are white or greenish. In open, sunny thickets many plants of *Aralia hispida* grow together and produce numerous umbels of inconspicuous flowers with small white petals. The honey is abundant and freely exposed, and I have collected upon the flowers eighty-two visitors. Bees, with the exception of the honeybee, are not common; but the less specialized Hymenoptera, such as ichneumon flies and wasps, are numerous. Notwithstanding their want of bright colors, the flowers are very attractive to the butterfly *Argynnis aphrodite*, several of which may often be seen at work on the same plant. Though *A. racemosa* may be found growing but a short distance from *A. hispida*, its habitat is within the precincts of shady woods, where the greenish flowers attract a much smaller circle of guests. The green flowers of *A. nudicaulis* (wild sarsaparilla) are also visited by few insects. The color of *A. hispida* appears to be of slight

importance in attracting insects, compared with its sunny, sheltered location and easily accessible supply of honey.

Few plant families have attained a form of inflorescence so well adapted to insure cross-fertilization as the Umbelliferæ. To this family belong the caraway and carrot, the wild parsnip, the water hemlock, and parsley, — plants growing luxuriantly by the roadside, along the river, and in the meadow. There are about 1600 species, mostly confined to the temperate zone. The flowers differ very little in structure, and the species can be identified only by the mature fruit. The small flowers gain conspicuousness by aggregation, and by standing in the same horizontal plane afford a convenient landing place for insects, and admit of rapid fertilization. The honey is secreted in a thin layer by the fleshy disk surrounding the style. The number and variety of the visitors surpass those of all other families. In Germany there have been collected on the caraway 55, on the wild carrot 61, and on the wild parsnip 118 insects. Probably the number of visitors to many species exceeds 200; while there is thus ample provision for intercrossing, self-fertilization is in most species prevented by the anthers and stigmas maturing at different times. Admirable simplicity and perfection are here combined.

There are 58 white, 16 yellow, 1 purple, and 3 blue flowers. As in the Cruciferæ, which have also very uniform flowers, white and yellow predominate, red and purple are more rare. The 16 yellow flowers belong to 11 genera, only three of which contain more than one species. In his *Fertilization of Flowers* Müller enumerates 7 Diptera and 7 Hymenoptera collected on the dull-yellow flowers of *Pastinaca sativa;* 4 Diptera and 4 Hymenoptera on *Bupleurum falcatum;* 15 Diptera and 31 Hymenoptera on *Anethum graveolens;* and remarks, "So the dull-yellow flowers of this plant, *P. sativa*, like those of Bupleurum and Anethum, are visited only by Diptera and Hymenoptera, not by beetles." On page 574 he adds: "All dull-yellow, dirty-yellow, brownish-yellow, yellowish-white flowers, *Bupleurum anethum*, Pastinaca, *Rhus cotinus*, *Galium mollugo*, Ruta, Neottia, Euonymus, Euphorbia, Adoxa, Alchemilla, are entirely or almost entirely avoided by beetles. The only apparent

explanation of these facts is that beetles are only or mainly attracted to flowers by bright colors. If this explanation is correct, dull yellow must be an advantageous color for plants with freely exposed honey, protecting them from injurious guests." Subsequent observations of Müller himself showed that *Bupleurum falcatum* was very frequently visited by the beetle *Mordella pumila*. In Schlesien, Loew observed on *Anethum graveolens* 5 species of beetles; numerous beetles were observed in the Tyrol by Schultz on *Rhus cotinus*, and on Euonymus both Schultz and Knuth observed beetles. The writer has found beetles very frequent visitors to the dull-yellow flowers of *Acer spicatum*. These illustrations need not be carried further, as it is evident that more extended observations have disproved Müller's generalization that dull yellow excludes the visits of beetles.

In the Umbellales both yellow and white have probably been derived directly from the primitive green. The involucre of *Cornus canadensis* changes from green to white, and the petals of many species of Cornus are green in the bud but become white as the flowers expand, while in the Umbelliferæ greenish-yellow flowers occur. In Apium one of the species is greenish yellow and two others are white. In Sanicula, *S. gregaria* has yellow petals exceeding the calyx and bright-yellow anthers, and *S. marylandica* has very small greenish-white petals and anthers. In Peucedanum three species are yellow and one white. White flowers may in some instances have been derived from yellow, as it has been shown that the yellow petals change to white in individual flowers in the Cruciferæ. As regards attractiveness to insects the yellow flowers of the Umbelliferæ do not appear to possess any advantage over their white competitors.

In Thespium two of the species have yellow flowers, and in the third they are purple, with a common yellow variety. Many of the white species tend to become pink or reddish. In *Daucus carota* the central flower of the umbel, and frequently of the umbellets, is purple, and I have often seen the entire umbel pinkish. The coloration of this single flower can, of course, be of no advantage to the plant in attracting insects, and Darwin supposes that it is a relic of a former ancient condition. I am

inclined to believe that it is due rather to the chemical constitution of the soil and nutritive fluids and the action of light. The terminal flower receiving the greatest amount of sap would be the first affected, then those of the umbellets, and finally the entire umbel. The color changes of many flowers appear to be due to such causes rather than to the influence of insects. In Low Germany *Pimpinella magna* is white, and in the more intense light of the Alps pinkish. Both rose-colored and yellow flowers have been found on plants of *Eriogonum ovalifolium* growing in silver-ore localities. Chemical analysis showed that the rose flowers contained arsenic, which was not present in the yellow. As a stimulus in nutrition may intensify the color, so a check in growth may cause it to revert to white.

Increased conspicuousness of the umbel is gained in some genera by the enlargement of the outer petals of the marginal flowers, as in Heracleum. White bracts subtend the white flowers of Astrantia, and yellowish bracts the dull-yellow flowers of Bupleurum, and in Eryngium the flower stalk is colored.

The Cornaceæ include many ornamental shrubs valued for their bright-red bark, their variegated leaves, the masses of handsome flowers, and the coral and blue berries. The flowers are chiefly white, but in the European *Cornus mascula* are yellow. The forty or more small white flowers of the herbaceous bunchberry *Cornus canadensis,* gain conspicuousness by an involucre of four white bracts, sometimes tinged with red. I have also seen the leaves partially white. This species yields very little nectar, which can be detected only by close examination. The blooming season lasts for over a month, and the flowers are produced in the greatest profusion. I have watched these plants long and carefully, and have enumerated thirty-six visitors; but not once have bumblebees been seen to visit the blossoms, — a fact I attribute to the scarcity of honey. The shrubby species contain a more abundant supply of nectar. The cymes are large and very numerous, and not infrequently are sought by bumblebees. On *C. alternifolia* I have collected twenty-eight insects. There can be no doubt that the quantity and flavor of nectar is an element in the limitation of insect visits, but one that has received much less attention than

coloration. *C. florida* is provided with an involucre that is usually white, but varies to pink or red. The fruit is scarlet and the leaves are bright red in autumn.

SUMMARY.

1. Throughout the Choripetalæ, with few exceptions, conspicuousness is correlated with fertilization by insects. In the grape family the flowers depend upon their strong scent rather than upon bright coloring. In many genera it is possible to arrange the species in a progressive series, in which there is an advance from inconspicuousness, few visitors, and self-fertilization, to many visitors, great conspicuousness, and the loss of the power of self-fertilization. Pigments may be developed in all the organs of the inflorescence, as bracts, stems, sepals, petals, stamens, and pistils.

2. The green flowers of the Polypetalæ are small, and the petals are frequently wanting. The white and yellow flowers vary from small to large, are the most common, and contrast more strongly with the foliage than purple or blue. Of the seventy-one polypetalous families, forty-three contain white, forty-one yellow, and twenty-nine both kinds of flowers. White flowers are most common in families or genera containing shrubs and trees, small flowers aggregated in a dense inflorescence, and nocturnal flowers. Dark nocturnal flowers are strongly scented. Yellow flowers are more commonly herbaceous and are most abundant in the same families as white flowers, unless the species are shrubs or trees.

3. There is no evidence of the preference of beetles for flowers of any particular color. They do not avoid dull yellow. They are most common on small, white-clustered flowers with easily accessible honey and pollen. Diptera visit most frequently white and yellow flowers, but as they become more specialized and restrict themselves to flowers the percentage of visits to red and blue flowers increases. They appear to find a parti-colored, mottled, or dotted inflorescence, as in the Cruciferæ and Saxifragaceæ, attractive. Carrion flies prefer malodorous lurid-purple or flesh-colored flowers.

4. The changes of color and their sequence in individual flowers are noteworthy. Green changes to white (Cornus), to yellow (Thlaspi, Cardamine), to red (Hydrangea), to purple (Clematis), to violet (Cobæa); white changes to green (sepals of *Helleborus niger*), to yellow (Lantana), to red (Dianthus, *Hibiscus mutabilis*), to blue (many large blue flowers remain white until nearly ready to expand); yellow changes to white (Draba), to red (Æsculus), to blue (Myosotis); red changes to blue (Venetus and many Boraginaceæ); violet and blue may turn purple, green, or white in fading. The tendency of green, white, and yellow to change to red or blue is much stronger than the reverse.

5. The floral colors are often correlated with the colors of the stems and leaves, as in Sedum. The foliage of the plants with white flowers is, as a rule, paler than when the flowers contain pigments. The development of bright colors in autumn leaves presents a series of color changes, which are in part parallel to those which occur in flowers. With the disappearance of the chlorophyll the leaves become whitish, yellow, or red, according as the cells contain no pigment, or solid yellow granules, or red pigment dissolved in the cell sap. The leaves of many plants are yellowish green, due to the presence of a yellow pigment. Green, yellowish-green, and greenish-yellow flowers contain chlorophyll, and though usually small are occasionally of large size. Many white and yellow flowers are derived directly from the primitive green. White is usually a structural or optical color due to the unequal reflection and refraction of light by the intercellular air spaces and the cells devoid of pigment. White flowers are a less tax upon the energies of the plant. Flowers of all colors may revert to white, which is commonest in nature and most true to name under cultivation. If with the disappearance of the chlorophyll there is an insoluble yellow pigment in the cells, the petals are a pale yellow, and with its increase change to bright yellow or orange. The development of anthocyanin, or red pigment, dissolved in the cell sap, changes white flowers to red and yellow flowers to scarlet. With a decrease in the acidity of the cell sap the red flowers become blue. Müller's observations led him to the conclusion that the

honeybee prefers blue, violet, various shades of purple and red, to white and yellow, and avoids scarlet and lurid colors.

6. The formation of pigments is effected by the chemical composition of the soil, by altitude or the intensity of light, by latitude, and by the absence or presence of moisture, as well as other ecological forces. The particular coloration of flowers is largely a chemical problem.

The Colors of Northern Polypetalous Flowers.

Orders.	Families.	Green.	White.	Yellow.	Red.	Purple.	Blue.	Total.
Ranales	Nymphæaceæ		4	5	1	1		11
	Ceratophyllaceæ	1						1
	Magnoliaceæ		4	2				6
	Anonaceæ					1		1
	Ranunculaceæ	6	26	38	3	13	11	97
	Berberidaceæ		3	3		1		7
	Menispermaceæ	1	2					3
	Calycanthaceæ					2		2
	Lauraceæ	2		4				6
Papaverales	Papaveraceæ		5	10	6	2		23
	Cruciferæ	2	54	46	1	10		113
	Capparidaceæ		3	2	1	1		7
	Resedaceæ		1	2				3
Sarraceniales	Sarraceniaceæ			1		1		2
	Droseraceæ		4			1		5
Rosales	Podostemaceæ	1						1
	Crassulaceæ	2	2	5	2	2		13
	Saxifragaceæ	4	30	6		3		43
	Grossulariaceæ	4	6	1		2		13
	Hamamelidaceæ	1	1	1				3
	Platanaceæ	1						1
	Rosaceæ	4	35	39	13	4		95
	Pomaceæ		27		5			32
	Drupaceæ		20		1			21
	Mimosaceæ		3	1	2			6
	Cæsalpiniaceæ	2	1	7		1		11
	Krameriaceæ					1		1
	Papilionaceæ		39	33	13	88	24	197
Geraniales	Geraniaceæ		1		3	7		11
	Oxalidaceæ		1	6		1		8
	Linaceæ		1	6			2	9
	Zygophyllaceæ			2				2
	Rutaceæ	1	2					3
	Simarubaceæ	1						1
	Polygalaceæ		3	3	2	8		16
	Euphorbiaceæ	38	9	5	1			53
	Callitrichaceæ	4						4

THE COLORS OF NORTHERN POLYPETALOUS FLOWERS.

(*Continued.*)

ORDERS.	FAMILIES.	GREEN.	WHITE.	YELLOW.	RED.	PURPLE.	BLUE.	TOTAL.
Sapindales	Empetraceæ					2		2
	Buxaceæ	1						1
	Limnanthaceæ		1					1
	Anacardiaceæ	7		1				8
	Cyrillaceæ	1						1
	Ilicaceæ		10					10
	Celastraceæ	3		1		2		6
	Staphyleaceæ		1					1
	Aceraceæ	5		3	1			9
	Hippocastanaceæ		1	3	1			5
	Sapindaceæ		2					2
	Balsaminaceæ			2				2
Rhamnales	Rhamnaceæ	5	3					8
	Vitaceæ	13						13
Malvales	Tiliaceæ		3					3
	Malvaceæ		4	5	13	4		26
Parietales	Theaceæ		3					3
	Hypericaceæ			22	2			24
	Elatinaceæ	4						4
	Cistaceæ	9		5				14
	Violaceæ		7	6		4	17	34
	Passifloraceæ		1	1				2
	Loasaceæ		2	3				5
Opuntiales	Cactaceæ	1		7	1	3		12
Thymeleales	Thymeleaceæ			1		1		2
	Elæagnaceæ			3				3
Myrtales	Lythraceæ	2				10		12
	Melastomaceæ				1	3		4
	Onagraceæ	3	14	24	10	6		57
	Trapaceæ		1					1
	Haloragidaceæ	6			1	6		13
Umbellales	Araliaceæ	2	3	1				6
	Umbelliferæ		58	16		1	3	78
	Cornaceæ	3	9	1		1		14
	Total	140	410	333	84	193	57	1217